REVISION OF VERNONIA (COMPOSITAE), SUBSECTION PANICULATAE, SERIES UMBELLIFORMES OF THE MEXICAN HIGHLANDS

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Vernonia is a large genus of 800 to 1,000 species, particularly abundant in South America, in certain regions of Africa, southeast Asia, and in North America (Willis, 1966). Although relatively uniform in its floral morphology, Vernonia exhibits extreme diversity in its vegetative features and includes herbs, shrubs, small trees, and vines. Because of the sheer number of taxa in Vernonia and lack of knowledge of most species, natural subdivisions of the genus have only rarely been fully circumscribed.

Subsection Paniculatae series Umbelliformes of section Lepidapoa established by Gleason (1906) seems to be an exception and appears to be a natural grouping. Gleason noted that the branches of the panicle are mostly aggregated or separated by shortened internodes, the peduncles are approximately uniform in length, the heads appear in subumbellate clusters which are in turn united into large pyramidal or hemispheric inflorescences. The plants are herbaceous to suffruticose perennials. The 10 species appear closely related and all are found in the highland regions of Mexico.

Gleason (1906, 1922) recognized nine species and in this paper ten species and seven subspecies are treated with a greatly revised taxonomy. Keys, synonymies, descriptions, typifications, distribution maps and specimen citations are given for the taxa. A new species, V. cronquistii, is described from Guerrero and Oaxaca. Vernonia liatroides ssp. gentryi is described from Durango south to Jalisco. Several changes in rank are made: V. inuloides is reduced to V. karvinskiana ssp. inuloides; V. ehrenbergiana is treated as V. liatroides ssp. ehrenbergiana; and V. vernonioides is now V. seratuloides ssp. vernonioides.

During the past four years, six of the 10 species have been studied in the field and in the greenhouse. Chromosome numbers, sesquiterpene lactones, and flavonoids have been determined for some of the taxa and hybridization experiments have been carried out within the group and with certain other Vernonias. The cytogenetical and phytochemical data provided considerable information and insight into the systematics of the group and they are presently being prepared for separate publication and will only be briefly summarized here.

Vernonia alamanii, V. serratuloides, and the three subspecies of V. liatroides have the sesquiterpene lactone Glaucolide-A (Mabry, et al., 1975). This bitter compound is found in 10 species of the closely related subsection Paniculatae series Verae from eastern North America; it is found as well in several species from South America. The flavonoid chemistry of V. alamanii and V. liatroides is similar also to that of series Verae with one exception; a compound tentatively identified as 3, 3'-0- dicayl quercetin 7-0-glucoside is present in the series Umbelliformes but not in series Verae (Mabry, et al., 1975).

Seven of the 10 species are known chromosomally, each having n=17, the same as the 18 species of series Verae from eastern North America (Jones, 1974). Experimental hybridizations within and among our accessions of series Umbelliformes generally have yielded fertile F_1 hybrids, but crosses between members of series Umbelliformes and series Verae have yielded vigorous but sterile F_1 hybrids. The phytochemical and cytogenetical data, briefly summarized here, support Gleason's (1923) conclusions that these two series were derived from a common ancestral line.

The taxonomic treatment presented here represents a synthesis of the results of various systematic techniques, but the descriptive and revisionary aspects have been largely drawn from about 900 herbarium specimens borrowed from BM, DUKE, ENCB, F, GA, GH, K, LD, MEX, MINN, MO, NY, P, TEX, UC, UMO, and US.

ACKNOWLEDGEMENTS

I wish to especially thank the curators of the herbaria who loaned specimens of *Vernonia* used in this study. Drs. Caywood Chapman, Bill Burnett, and Earl Parker, and my wife, Carleen A. Jones, accompanied me on field trips to Mexico. I would like to thank the Consejo Nacional de Ciencia y Tecnologia of México for allowing me to collect in Mexico. I am indebted to the editor of the Goode Base Map Series, the University of Chicago, for permission to use copyrighted base maps (copyright, the University of Chicago, Department of Geography). This work was supported by National Science Foundation Grant GB20687 and by the University of Georgia.

KEY TO THE SPECIES

- 1. Peduncles multi-bracteate throughout with short bracts 1-2 mm long, similar to the outer phyllaries; heads 3-5 flowered; outer phyllaries glandular-tomentose; rare and local from the state of Tepic. 10. V. feddemae
- 1. Peduncles not bracteate or with only one or two bracts over 2 mm long, not similar to the outer phyllaries; heads (4) 5 or more flowered; outer phyllaries glabrate to glandular or slightly pubescent.
 - 2. Involucre height 13-24 mm, width 11-18 mm. 1. V. alamanii
 - 2. Involucre height 4-12 (15) mm, width 3-12 mm (14).
 - 3. Achenes pilose to pilose-hispid or ciliate on the ribs.
 - 4. Heads with over 50 flowers. . . 9. V. barclayi
 - 4. Heads with less than 20 flowers.
 - 5. Heads (4) 5-6 (7) flowered; leaf blades 20-30 cm long, 6-15 cm wide; inner phyllaries acuminate. 7. V. autumnalis
 - 5. Heads 10-14 (18) flowered; leaf blades 6-14 (16) cm long, 2-9 cm wide; inner phyllaries acute to cuspidate.

- 6. Leaf blades tomentose to hirsute-villous beneath; distributed from Oaxaca to Chiapas. 5. V. oaxacana
- 3. Achenes glabrate to glandular or resinous-glandular.
 - 7. Outer phyllaries long-acuminate terminating gradually in a sharp point, (2) 3-6 mm long, tips 1-3 mm long. 8. V. bealliae
 - 7. Outer phyllaries acute, acute-acuminate, or apiculate to bitten, not terminating gradually into a sharp point, 0.8-2.5 mm long, tips less than 1.5 mm long.

 - 8. Heads 8-20 (25) flowered; inner phyllaries acute, sometimes slightly apiculate, or mucronate.
 - 9. Leaf blades 2-14 cm wide, ovate-lanceolate to lanceolate, length/width ratio 2-3. 3. V. liatroides
 - 9. Leaf blades 1-3 cm wide, oblong to linear-lanceolate, length/width ratio (2.2) 3-8. 6. V. serratuloides
- 1. Vernonia alamanii DC. Prodr. 5: 61. 1836. TYPE: México: Alaman 1831 (Holotype: G-DC, as photo F! us! as IDC microfiche G-DC!).

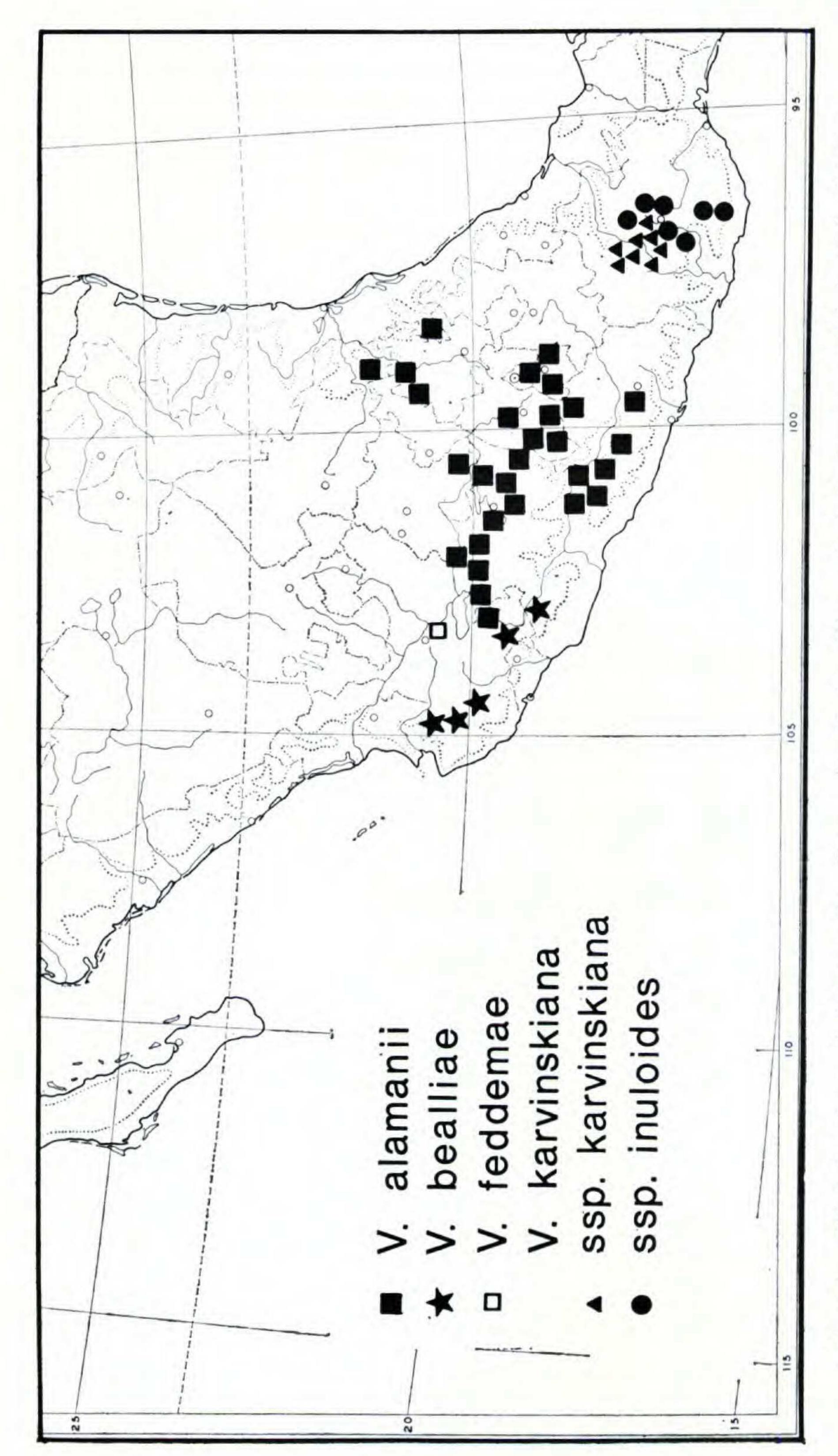
Cacalia alamanii (DC.) Kuntze, Rev. Gen. Pl. 2: 969. 1891.

Vernonia dictyophlebia Gleas. Bull. New York Bot. Gard. 4: 203. 1906. TYPE: México: Michoacán: Hills of Patzcuaro, Pringle 3347 (Holotype: NY! Isotypes: BM! ENCB! F! GH! K! MEX! MINN! MO! NY! P! UC! US!).

Vernonia alamanii DC. var dictyophlebia (Gleas.) Mc-Vaugh, Contrib. Univ. Michigan Herb. 9: 477. 1972.

Suffruticose, 1-2 m tall; stems floccose, becoming glabrate below. Leaves cauline; leaf blades 8-14 cm long, 3.5-7 cm wide (length/width ratio ca. 2.2), widest below the middle, ovate, ovate-lanceolate, to lanceolate, scabrous above, veiny and either glabrous or pilose-hispid below, apically acute, basally cuneate, margins serrate; petioles 7-33 mm long, floccose. Inflorescences hemispheric or depressed, variable in size. Heads (43) 51-65 (76) flowered; peduncles 2-4 cm long, floccose, aggregated into clusters. Involucres campanulate, 13-24 mm high, 11-18 mm wide; phyllaries glabrous, margins fimbriate, loosely imbricated, outer reflexed, greenish to brownish-purple; inner phyllaries linear to linear-spatulate, 11-19 mm long, 1.5-4 mm wide, tips mucronate-aristate, mucro 0.3-3.5 mm long; outer phyllaries linear to lanceolate or ovate, 4.5-9 (11) mm long, 1.5-3.2 (4) mm wide. Pappus straw-colored; inner bristles (6) 7-11 mm long, outer bristles 0.8-1.7 mm long. Corollas (9.6) 12-19 (21) mm long, reddish-purple. Anthers 3-5 (6.1) mm long. Achenes 3-4.5 mm long, densely white glandular, ca. 10 ribbed, basally terminating in a prominent yellow areola. Chromosome number n=17. Flowering and fruiting occur from November to February (April).

This species is distributed from San Luis Potosí to Jalisco, Michoacán, and Guerrero as shown in Fig. 1. It grows on rocky limestone or volcanic hillsides, fields and roadsides in the oak-pine zone from ca. 1,800 to 2,600 m altitude. This species is centered on the Neo Volcanic Plateau and extends southward into the Sierra Madre del Sur and northward into the Sierra Madre Oriental. Gleason recognized two species but as McVaugh (1972) pointed out, they are not separable on the basis of lower leaf surface. McVaugh's use of the length of the phyllary awns breaks down when one examines a large sample of specimens. The specimens from Michoacán tend to have broader and more pubescent leaves but even this is highly variable.



REPRESENTATIVE SPECIMENS: México: San Luis Potosí: ca. 10 mi W Xilitla, hwy 120, King 4438 (F, MICH, TEX, UC, US); Hidalgo: 9 mi NE Jacala, hwy 85, King 4216 (F, MICH, TEX, UC, US); Veracruz: Huayacocotla, R. Hdez M. & Vazquez de Hdez 986 (GH); Guanajuato: Acámbaro, Rzedowski 25349 (MICH); Jalisco: Mazamita, Díaz Luna 3164 (ENCB); Michoacán: Zitacuraro-Zirahuato, Hinton 13541 (GH, MICH, TEX, UC); México: Temascaltepec, Hinton 8881 (MICH, TEX, UC, US); DF: Canada of Contreas, Pringle 15034 (F, MICH, MIN, MO, TEX); Morelos: Mountain side above Cuernavaca, Pringle 8045 (F, GH, MEX, MICH, MIN, UC); Guerrero: San Antonio-Buenos Aires, Montes de Oca, Hinton 14071 (GH, MICH, TEX, UC, US).

Natural hybridization occasionally occurs between Vernonia alamanii and V. liatroides ssp. ehrenbergiana. Hybrid specimens examined include: México: México: Pineda, Temascaltepec, Hinton 3187 (NY, GH); Nanchititla, Temascaltepec, Hinton 7546 (K, US); Michoacán: 12 mi NW of Morelia on hwy 15, Jones 20574 (GA).

One putative hybrid between *V. alamanii* and *V. liatroides* ssp. *liatroides* was collected: México: Hidalgo: 0.3 mi N km 150 hwy 85, 11 mi S of State Line, *Chapman* 63 (GA).

2. Vernonia karvinskiana DC. Prodr. 5: 62. 1836. TYPE: México: Karwinski s.n. (Holotype: G-DC, as IDC microfiche G-DC!; isotypes: P! M, as photo NY! US!).

Ascending, suffruticose perennial, 1-3 m in height; stems glabrate to hispid or floccose. Leaves cauline; upper leaf blades (4.5) 6-10 (11.5) cm long, (0.5) 2-5 (6) cm wide (length/width ratio ca. 2-3), widest at or below the middle, lanceolate to ovate, scabrous above, glabrate to floccose below, apically acute to acuminate, basally cuneate or sometimes rounded-truncate, margins serrate to almost entire; petioles 2-11 mm long, hispid to glabrate or floccose. Inflorescences pyramidal, variable in size but often 1 dm across. Heads 20-60 (70) flowered; peduncles 1-3 cm long, glabrate or pilose to floccose, subumbellate. Involucres vase-shaped, (7) 8-13 (15) mm high, 6-12 (14) mm wide; phyllaries glabrous to resinous, loosely appressed, dark purple to greenish; inner phyllaries lanceolate to linear-

oblong, (6) 7-11 (12) mm long, 1.3-2.6 mm wide, tips emarginate with a mucro in the notch, sometimes bitten or apiculate; outer phyllaries lanceolate, 2.2-6 mm long, 0.7-2.5 mm wide. Pappus straw-colored; inner bristles 5.2-7 mm long, outer bristles 0.5-2 mm long. Corollas (8) 9-12 (13.5) mm long, reddish-purple. Anthers 2.8-4.5 (5) mm long. Achenes 3-4.3 mm long, furrows often glandular, ca. 9 or 10 ribbed. Chromosome number n = 17. Flowering and fruiting occur from Sept. to Feb. (Mar.).

This species is restricted to the state of Oaxaca. It grows on rocky hillsides, moist mountain slopes, ridges, or disturbed grassy areas in full sun or partial shade of oak or pine-oak woodlands at an altitude of 1700-2100 m.

Two subspecies are recognized. Their distributions are shown in Fig. 1. They may be characterized and distinguished by the following key:

2a. Vernonia karvinskiana DC. ssp. karvinskiana.

Vernonia corymbiformis DC. Prodr. 5: 62. 1836. TYPE: México: Karwinski s.n. (Holotype: G-DC, as IDC microfiche G-DC! Isotypes: P! M, as photo NY! US!). (not Gleas. Bull. New York Bot. Gard. 4: 198. 1906).

Cacalia karvinskiana (DC.) Kuntze, Rev. Gen. Pl. 2: 970. 1891.

Cacalia corymbiformis (DC.) Kuntze, Rev. Gen. Pl. 2: 969. 1891.

Vernonia conzattii Robins. Proc. Amer. Acad. 44: 615. 1909. TYPE: México: Oaxaca: Sta. Ines del Monte, Zimatlan, Conzatti 1327 (Holotype: GH! Isotype: MEX!).

This subspecies is common in the oak woodlands of the Sierra Madre de Oaxaca. It intergrades with ssp. *inuloides* in the Altiplano de Oaxaca.

REPRESENTATIVE SPECIMENS: México: Oaxaca: Amongst dwarf oaks, dry hills above Las Sedas, 7,000 ft., *Pringle* 6019 (GH, MEX, MICH, MIN, MO, NY, P, UC, US); in oak woodland at summit about 15 km N of Telixtlahuaca on road to Tehuacan, Elev. 2100 m, *Cronquist & Fay* 10914 (NY, TEX, US).

2b. Vernonia karvinskiana ssp. inuloides (DC.) S. B. Jones, stat. nov.

Vernonia inuloides DC. Prodr. 5: 62. 1836. TYPE: México: Karwinski s.n. (Holotype: G-DC, as IDC microfiche G-DC!, as photo NY! US! Isotype: P!).

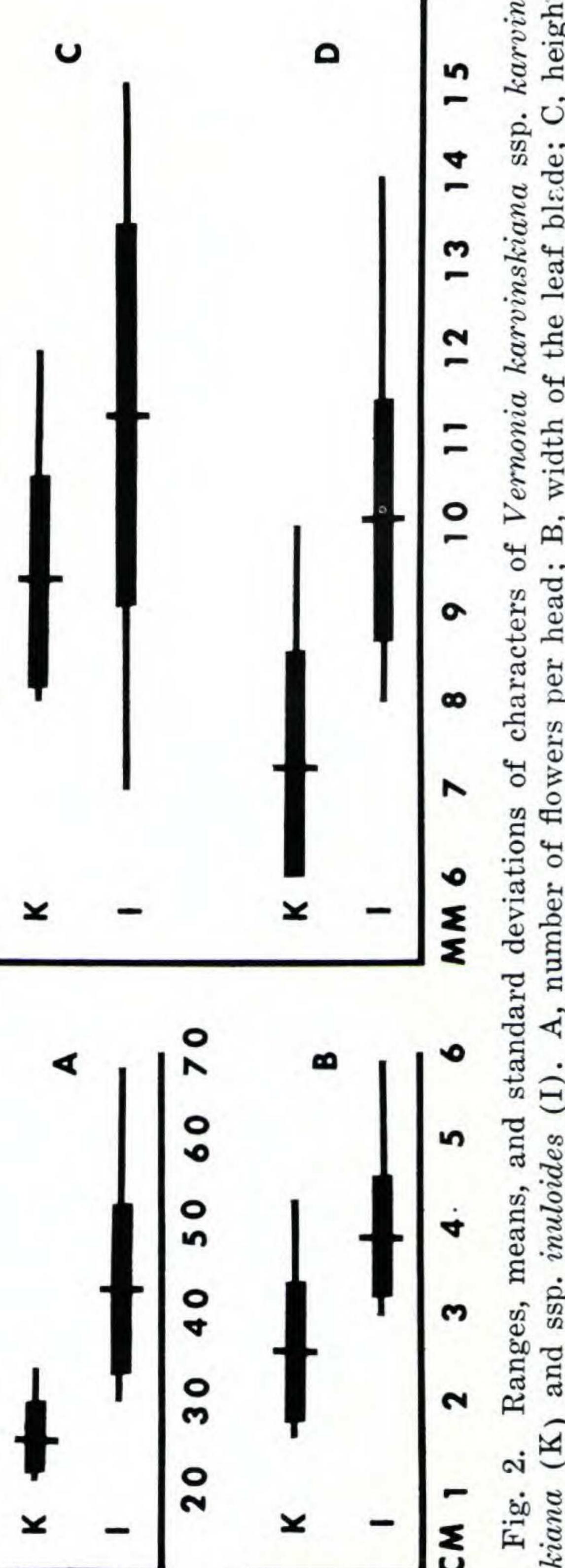
Cacalia inuloides (DC.) Kuntze, Rev. Gen. Pl. 2: 970. 1891.

This subspecies is common in the oak-pine woodlands of the Altiplano de Coatlan and the Altiplano de Mixtepec northward into the Altiplano de Oaxaca.

REPRESENTATIVE SPECIMENS: México: Oaxaca: 12 miles S of Sola de Vega and 90 miles N of Puerto Escondido, Cronquist & Sousa 10504 (GH, MEX, MICH, NY, TEX); 80 miles S of Oaxaca, S of Miahuatlán, Cronquist & Sousa 10445 (GH, MEX, MICH, NY).

A splitter perhaps would have recognized two species; however the differences between these two taxa are more apparent than real. Sixteen morphological features were measured or scored on 25 herbarium specimens of each taxon; most were not useful as key characters. The most distinctive features are compared in Fig. 2 where their overlap is readily apparent. The morphological variation of the two subspecies was undoubtedly reinforced by their geographical isolation. Subspecies karvinskiana occurs in the mountains to the north of the city of Oaxaca and ssp. inuloides is centered in the mountains south of there; in between they intergrade completely. The close relationship of these two taxa is best shown by treatment at the rank of subspecies. If treated as two distinct species this relationship is likely to be obscured.

3. Vernonia liatroides DC. Prodr. 5: 34. 1836. TYPE: México: Tamaulipas: Tula to Tampico, Berlandier 2139 (Holotype: G-DC, as IDC microfiche G-DC! as photograph US! Isotypes: GH! NY! P!).



and ssp. inuloides (I). A, number of flowers per head; B, width of the leaf blacre; D, width of the involucre.

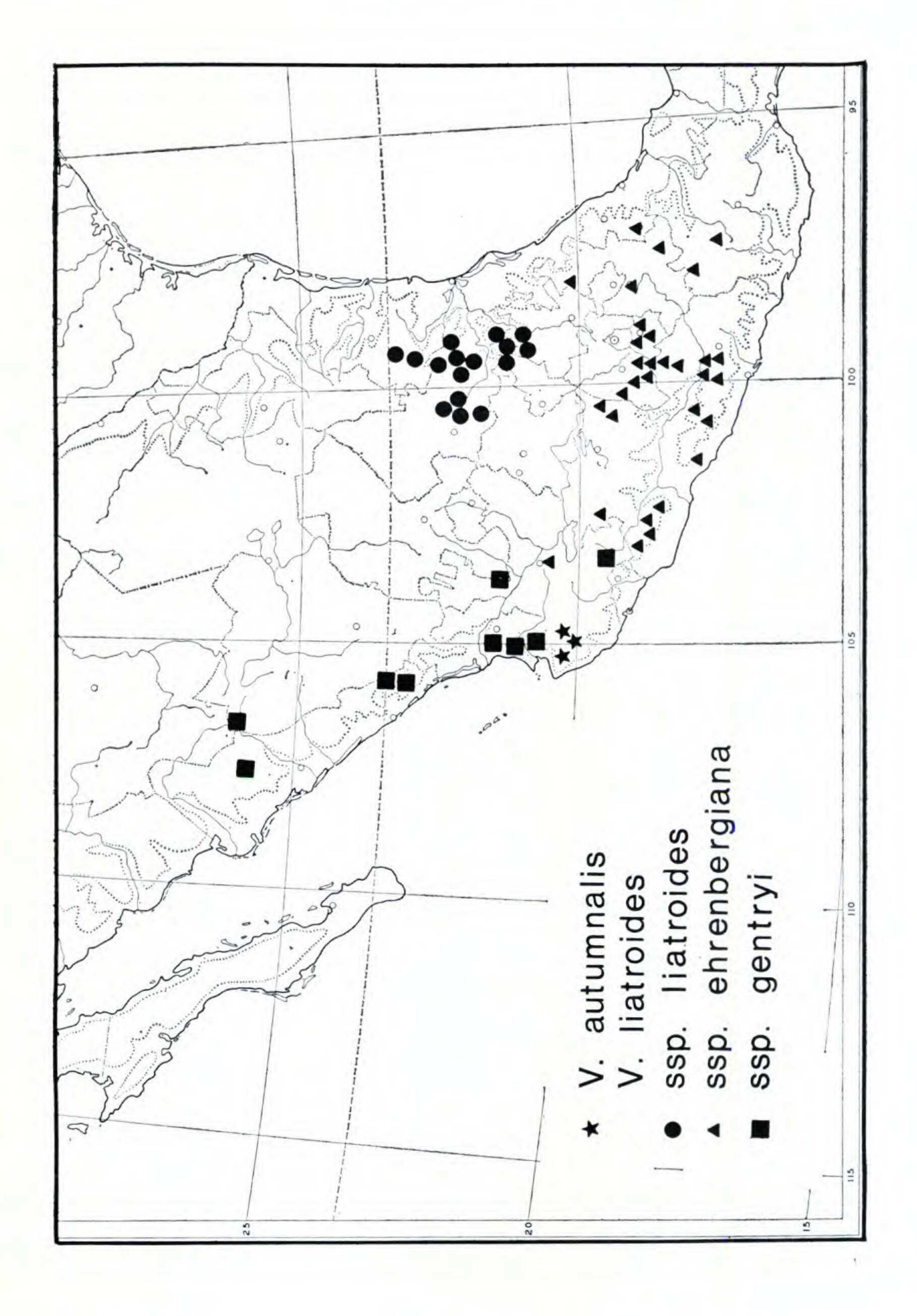
Herbaceous perennial, sometimes becoming frutescent, 1-3 m; stems pilose-hispid or sometimes glabrate. Leaves cauline; leaf blades 4.5-25 cm long, 2-14 cm wide (length/ width ratio ca. 2-3), widest at the middle, lanceolate or ovate-lanceolate, slightly scabrous or almost glabrate above, punctate, pilose-hispid, or glabrate below, apically acute, basally cuneate, margins serrate; petioles 0.4 to 3.5 cm long, downy to glabrate. Inflorescences narrowly pyramidal to broadly pyramidal. Heads (8) 9-20 (25) flowered; peduncles 3-5 mm long, downy to glabrate, subumbellate. Involucres campanulate, (3.7) 4.5-6.5 (8) mm high, (2.8) 4-6 (7.5) mm wide; phyllaries ciliate, loosely appressed, greenish-purple sometimes shiny; inner phyllaries oblonglanceolate, (3.2) 4-5 (6) mm long, (0.8) 1-1.5 (1.7) mm wide, tips acute, slightly apiculate; outer phyllaries lanceolate, (0.8) 1.3-2.3 (2.5) mm long, 0.5-1.2 (1.8) mm wide. Pappus whitish; inner bristles 4.5-6.4 mm long, outer bristles 0.8-1.5 mm long. Corollas (5) 6-10 (11) mm long, reddish-purple to light pink, fading to almost white, glabrous, very fragrant. Anthers 2-4 mm long. Achenes 2-3.2 mm long, resinous glandular or sometimes glabrous, ca 10 ribs. Chromosome number n=17. Flowering and fruiting occur from October to May.

This species is distributed from the Sierra Madre Oriental south and west across the Neo Volcanic Plateau and northward along the Sierra Madre del Sur and the Buried Ranges and Sierra Madre Occidental.

Three subspecies are recognized. Their distributions are shown in Fig. 3. They may be characterized and distinguished by the following key:

Plants normally flowering from October to December, from the Sierra Madre Oriental, or the Neo Volcanic Plateau and the Sierra Madre del Sur; leaf blades (4) 5-11 (13) cm long, 2-5 (7) cm wide, petioles 0.3-1.3 cm long; flowers per head (8) 9-13 (17).

Fig. 3. Distribution of Vernonia autumnalis and V. liatroides.



Plants from the Sierra Madre Oriental, frutescent herbaceous perennial; corolla lobes (2.2) 2.5-3.5 (4.2) mm long, corolla (5.5) 7-9 mm long. . 3a. ssp. *liatroides*

3a. Vernonia liatroides ssp. liatroides.

Eupatorium tulanum Klatt, Abh. Nat. Ges. (Halle) 15: 323. 1882. TYPE: México: Tamaulipas: Tula to Tampico, Berlandier 2139 (Holotype GH! Isotypes: G-DC, as IDC microfiche G-DC! P!).

Cacalia liatroides (DC.) Kuntze, Rev. Gen. Pl. 2: 971. 1891.

This subspecies is common on limestone hillsides, in mesic habitats of the Sierra Madre Oriental in the tropical deciduous forest up and into the pine-oak zone. Flowering and fruiting normally occur from October to January. The plants become woody near the base of the stems.

REPRESENTATIVE SPECIMENS: México: Tamaulipas: Viereck s.n. (US); San Luis Potosí: 19 mi WSW Xilitla, hwy 120, oak-pine forest, red limestone soil, Jones 22376 (GA); Hidalgo: 27 mi S Tamazunchale at Santa Maria, shrub 2 m. tall, rocky hillside, Jones 20560 (GA); Queretaro: 5 mi WSW Jalpan, hwy 120, abundant along limestone roadsides, Jones 22378 (GA).

3b. Vernonia liatroides ssp. ehrenbergiana (Sch. Bip.) S. B. Jones, stat. nov.

Vernonia ehrenbergiana Sch. Bip. Linnaea 20: 513. 1847. TYPE: México: Barranco pr. los reyes, Ehrenberg 710 (Holotype P!).

Cacalia ehrenbergiana (Sch. Bip.) Kuntze, Rev. Gen. Pl. 2: 971: 1891.

Vernonia capreaefolia Gleas. Bull. N.Y. Bot. Gard. 4: 200. 1906. TYPE: México: Veracruz: Orizaba, Schaffner 117 (Holotype: GH!).

This subspecies is commonly found along roadsides and on rocky hillsides in the Neo Volcanic Plateau and the Sierra Madre del Sur. In the latter region it is often associated with limestone. It appears to be a herbaceous perennial, unlike the other two subspecies which become suffrutescent. Subspecies *ehrenbergiana* and ssp. *gentryi* intergrade in western Jalisco. Flowering and fruiting occur from October to January.

REPRESENTATIVE SPECIMENS: México: Jalisco: Guadalajara, Pringle 2943 (GH); Michoacán: km 115 hwy 15 between Zitacuaro and Cd. Hidalgo, Jones 20572 (GA); Guerrero: 8 km SW Xochipala, Feddema 2765 (ENCB, MICH, TEX); México: 2 mi N Ixtapan de Sal hwy 55, Jones 20569 (GA); Oaxaca: Huajuapam, Nelson 1979 (GH, US); Puebla: by streams near Tehuacan, Pringle 6246 (BM, ENCB, F, GH, MEX, MIN, P, UC, US); Veracruz: Orizaba; Bourgeau 3339 (F, GH, K, US).

3c. Vernonia liatroides ssp. gentryi S. B. Jones, ssp. nov. TYPE: México: Durango: 116 mi W of Durango on hwy 40, elev. 2000 m, *Jones* 22527 (Holotype: GA!).

Folia 10-25 cm longa, 5-15 cm lata (ratione longitudinis cum latitudine 1.5-2.5), ovali-lanceolata, vel lanceolata. Capitula (11) 13-18 (25) flora.

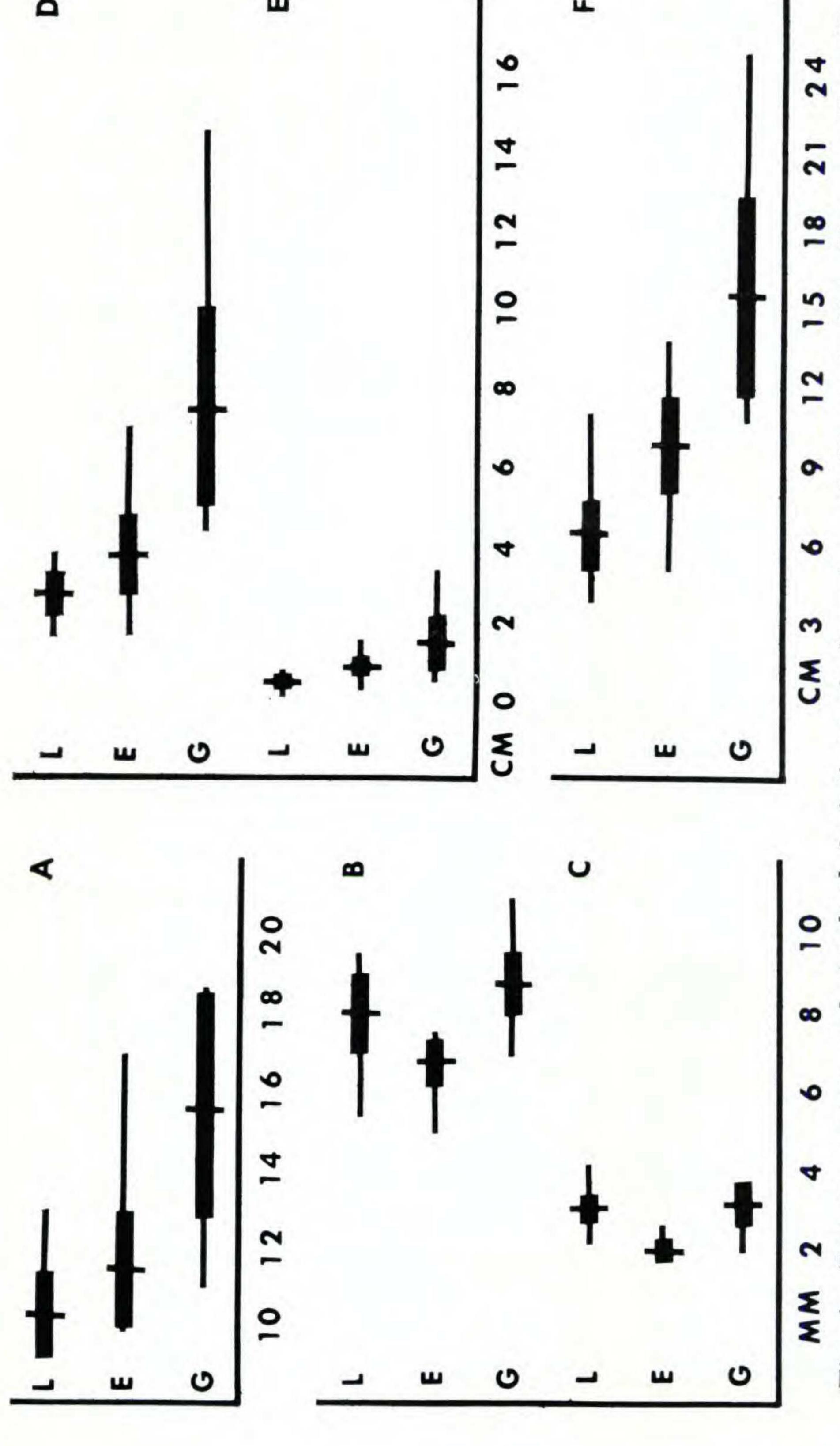
This subspecies is abundant at elevations of ca 1,500 to 2,000 m on the mesic west slopes in the pine-oak zone down into the tropical deciduous forests of the Buried Ranges and the Sierra Madre Occidental. It is named in honor of Howard Scott Gentry, whose collections from northwest Mexico have facilitated my studies of this and other species of *Vernonia*. Flowering and fruiting occur from March to May.

REPRESENTATIVE SPECIMENS: México: Durango: San Ramón, Palmer 140 (F, GH, MO, NY, US); Sinaloa: 132 mi W Durango near El Batel on hwy 40, Jones 22528 (GA); Nayarit: 15 km W Tepic, sobre el camino a Jalcocotán, Rzedowski 15614 (ENCB, MEX, MICH). Jalisco: San Sebastian, Hacienda del Ototal, Mexia 1681 (BM, F, GH, MICH, MIN, MO, NY, UC, US); Zacatecas: 5 mi SW Mezquital del Oro, McVaugh 22135 (ENCB, MICH, NY).

Nineteen morphological features were measured on 25 specimens of each of the three taxa. The measurements in general showed considerable overlap; however, those presented in Fig. 4 are of some diagnostic value. Keeping in mind the many features shared by these three taxa, they are best treated as subspecies.

4. Vernonia cronquistii S. B. Jones, sp. nov. TYPE: México: Guerrero: semi-open slopes in pine-oak forest in the mountains along the highway ca. 62 rd miles N of Acapulco, and 20 mi S of Chilpancingo, *Cronquist* 9705 (Holotype: NY! Isotypes: GH! MEX! MICH! MO! NY!).

Herba perennis, erecta, 1.5-metralis; caules purpurei necnon glabri. Folia caulina (6.5) 8-12 (15) cm longa, 1.9-4.5 cm lata (ratione longitudinis cum latitudine ca. 3-4), ad medium dilatata, ovato-lanceolata, supra scabridiuscula, infra glabrescentia, apicibus acuminatis, basibus anguste cuneatis, marginibus serratis; petioli 0.5-1.2 cm longi glabrescentes. Inflorescentiae paniculatae-umbellatae. Capitula 10-14 (18)-flora, cum pedunculis 0.5-1.3 cm longis. Involucra anguste campanulata 5.5-8.5 mm longa, 3-7.5 mm lata; phyllaria ciliata, laxe imbricata, purpurea, eis interioribus lineari-lanceolatis, 4.2-7.5 mm longis, 0.9-1.5 mm latis, apicibus acutis vel cuspidatis, eis exterioribus lanceolatis, 1-2 mm longis, 0.6-0.9 mm latis. Pappi setae albae, eis interioribus 5-6.1 mm longis, eis exterioribus 0.6-1.1 mm longis. Corollae (7.3) 9-11 (12.6) mm longae, Vernoniapurpureae, glabrae. Antherae 2.7-3.3 mm longae. Achaenia 2.2-3.1 mm longa, piloso-hispida, ca. 9-11 nervata. Chromosome number n=17. Flowering and fruiting occur from October to December. This species is dis-



number of flowers per head; B, lengt liatroidesRanges, means, and standard deviations of characters of Vernonia liatroide ventryi (G); ssp. ehrenbergiana (E); A, number of flowers per head; B, leng f the lobes of the corolla; D, width of the leaf blade; E, length of the petiole;

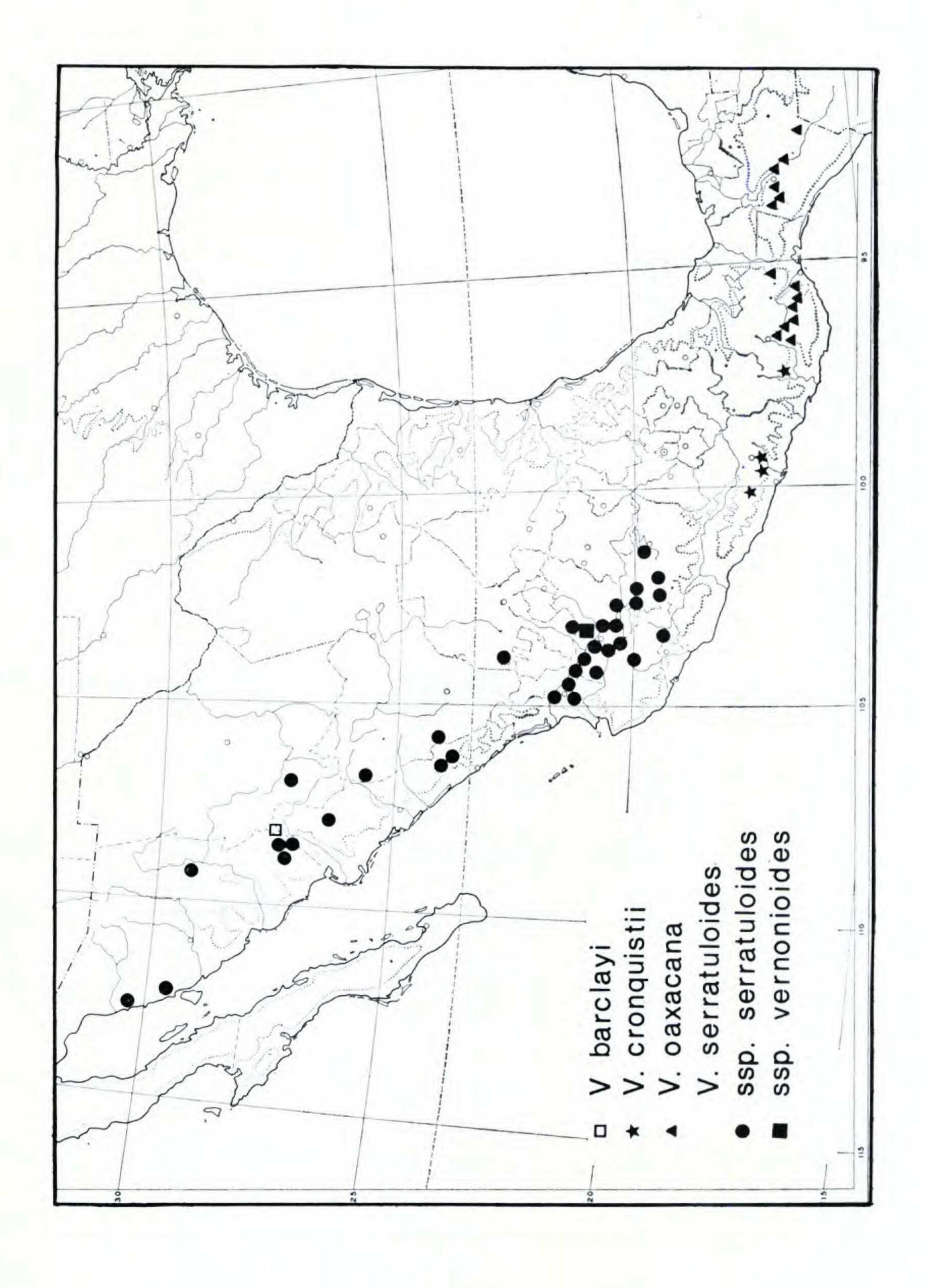
tributed from Guerrero to Oaxaca along the Sierra Madre del Sur as shown in Fig. 5. It occurs on semi-open slopes in pine-oak or pine forests at elevations of 700-950 m. It is named in honor of Dr. Arthur Cronquist who made the type collection and has provided encouragement to me with my studies of *Vernonia*.

Additional specimens examined include: México: Guerrero: Rincón de la Via, Kruse 739 (ENCB); Plan de Carrizo, Galeana, Hinton 11035 (GH, K, MICH, NY, US); Oaxaca: 5-6 km NE Putla rd to Tlaxiaco, McVaugh 22273 (ENCB, MICH).

5. Vernonia oaxacana Sch. Bip. ex Klatt, Leopoldina 20: 74. 1894. TYPE: México: Chiapas: San Carlos, Liebmann 49 (Syntypes: C, as IDC microfiche!, as photo and fragment US!, as photo F! NY! US!, as drawing and fragment GH!, as fragment P!).

Suffruticose, 0.5-2.5 m; stems hirsute-villous to tomentose, becoming glabrate with age. Leaves cauline; upper leaf blades 6.5-14 cm long, 2.4-8.7 cm wide (length/width ratio ca. 2), widest below the middle, elliptic-ovate, pilosehispid above, tomentose to hirsute-villous below, apically acute, basally oblique to cuneate or rounded, margins serrate; petioles 0.7-2 cm long, villous. Inflorescences pyramidal, large, irregular, highly branched, with many leaves. Heads (10) 11-13 (15) flowered; peduncles 5-10 mm long, hispid, appearing subumbellate. Involucres campanulate, (5.3) 6-7 (8) mm high, 4.2-6.6 mm wide; phyllaries glabrous, loosely appressed, greenish purple; inner phyllaries oblong-lanceolate, 4.2-6.7 mm long, 0.8-1.5 mm wide, tips narrowly cuspidate; outer phyllaries lanceolate, 0.7-2.2 mm long, 0.3-1 mm wide. Pappus white; inner bristles 5-6.5 mm long, outer bristles 0.9-2.2 mm long. Corollas (7) 8-9 (10) mm long, reddish-purple. Anthers 2.5-3.5 mm long.

Fig. 5. Distribution of Vernonia barclayi, V. cronquistii, V. oaxacana and V. serratuloides.



Achenes 2-3.2 mm long, sparsely ciliate on ribs, rarely glandular, ca. 10 ribs. Chromosome number n=17. Flowering and fruiting occur from Dec. to Feb.

This species is distributed from Oaxaca to Chiapas as shown in Fig. 5. This species grows in oak woodlands and on rocky roadsides at elevations of 900-1300 m.

REPRESENTATIVE SPECIMENS: México: Oaxaca: Along hwy 190, 67 mi W Tehuantepec, King 2476 (MICH, TEX, US); Chiapas: Roadside in low valley with palms, hwy 190, 15 mi S LaTrintaria, Breedlove & Raven 8433 (F, MICH).

6. Vernonia serratuloides H.B.K. Nov. Gen. Sp. 4: 33. 1818. TYPE: México: Michoacán: "Crescit regione temperata prope urbem Valladolid de Mechoacan, alt. 1000 hex." [Collector?] (Holotype: P, as photo F! as fragment P!).

Herbaceous perennial, ca. 1 m; stems glabrate to pilosehispid or rarely downy. Leaves cauline, crowded; leaf blades (5.2) 6-12 (13.5) cm long, (0.8) 1-3 (3.8) cm wide (length/width ratio ca. 2.2-8), widest at or below the middle, oblong to linear-lanceolate, scabrous or sometimes glandular-punctate or glabrate above, glandular-punctate or scabrous to pilose-hispid below, apically acute, basally cuneate, margins remotely toothed; petioles 2-5 mm, glabrate to pilose-hispid. Inflorescences narrowly pyramidal. Heads 9-19 flowered; peduncles 3-8 mm long, pilose-hispid to almost downy, subumbellate. Involucres narrowly campanulate, 6-9 mm high, (4) 4.5-9 (10) mm wide; phyllaries ciliate or hirsute to almost glabrate on the margins, tightly appressed, greenish to purple; inner phyllaries oblonglanceolate, 5-8 mm long, 1-1.5 mm wide, tips acute, sometimes with a small mucro; outer phyllaries lanceolate, 1.3-2.9 mm long, 0.5-1 mm wide. Pappus straw colored; inner bristles 5-6.5 mm long, outer bristles 0.4-1.2 mm long. Corollas 7.4-11 mm long, reddish-purple. Anthers 2.9-3.7 mm long. Achenes 2.5-3.3 mm long, glabrate to resinousdotted, 9-11 ribs. Chromosome number n=17. Flowering and fruiting occur from Sept. to Dec.

This species is distributed from Sonora southeastward into Jalisco and Michoacán as shown in Fig. 5. It grows on rocky hillsides, dry pastures, oak or oak-pine woodlands, fallow fields, often in sticky clay soil at altitudes of 300-1000 m. The range of this species is associated with the Sierra Madre Occidental and the northwestern part of the Neo Volcanic Plateau.

Two subspecies are recognized. They may be characterized and distinguished by the following key:

6a. Vernonia serratuloides ssp. serratuloides.

Vernonia sinclairi Benth. Bot. Voy. Sulph. 109. 1845. TYPE: México: Nayarit: San Blas-Tepic, Sinclair s.n. (Holotype K!).

Perezia paniculata Gray, Proc. Amer. Acad. Arts 21: 393. 1886. TYPE: México: Chihuahua: Mountains above Batopilas at the Frailes, ca. 7,000 ft, Palmer 279 (Holotype: GH! Isotypes: BM! US!).

Cacalia serratuloides (H.B.K.) Kuntze, Rev. Gen. Pl. 2: 970. 1891.

Cacalia sinclairi (Benth.) Kuntze, Rev. Gen. Pl. 2: 970. 1891.

Vernonia umbellifera Gleas. Bull. New York Bot. Gard. 4: 199. 1906. TYPE: México: Jalisco: Plains of Guadala-jara, Pringle 2316 (Holotype: NY! Isotypes: BM! F! MEX! MO! NY! P! UC! US!).

Vernonia camporum M. E. Jones, Contrib. West. Bot. 18: 69. 1933. TYPE: México: Jalisco: Orendain Nov. 27, 1930, M. E. Jones s.n. (Holotype: POM, as photo and fragment US!).

This subspecies is widespread with many collections from the southern part of its range. As to be expected there is some local variability but it is not sufficient to warrant recognition of additional taxa.

REPRESENTATIVE SPECIMENS: México: Sonora: Sierra de Alamos, Gentry 4862 (MICH, MO, NY, US); Chihuahua: rd. from Parral to Batopilas, Goldman 156 (US); Sinaloa: NW base of Cerro Colorado, Gentry 5192 (NY); Durango: Tamazula, Ortega 4443 (US); Nayarit: Laguna Santa Maria del Oro, Windler 2904 (MICH); Jalisco: Hills near Etzatlan, Pringle 11607 (F, MICH, MO, US); Michoacán: ca. 5 mi N Cotija and 22 mi S Jiquilpan, King & Soderstrom 4592 (MEX, MICH, NY, TEX, UC, US).

6b. Vernonia serratuloides ssp. vernonioides (Gray) S. B. Jones, stat. nov.

Perezia vernonioides Gray, Proc. Amer. Acad. Arts 22: 433. 1887. TYPE: México: Rio Blanco, in shady grassy bottoms, Palmer 745 (Holotype: GH!).

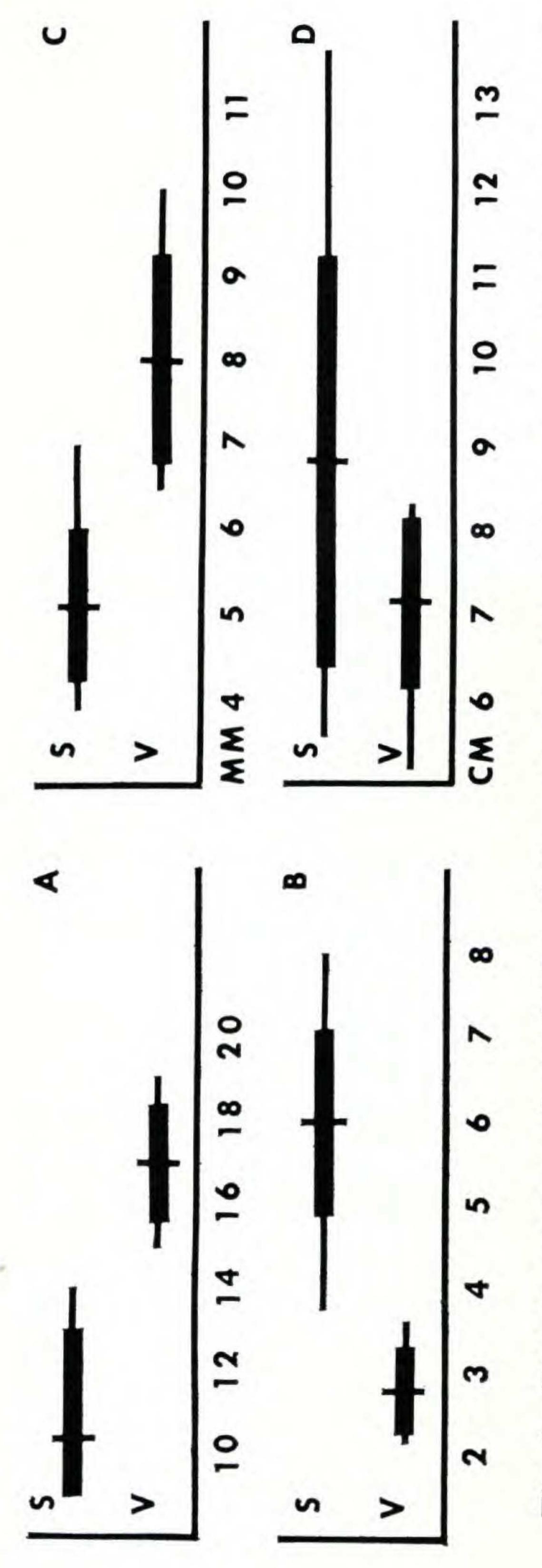
Vernonia vernonioides (Gray) Bacigal. Contr. Gray Herb. 97: 77. 1931.

Vernonia jaliscana Gleas. Bull. New York Bot. Gard. 4: 198. 1906. TYPE: México: Jalisco: Hills near Guadala-jara, 5,000 ft., Pringle 9994 (Holotype: GH! Isotypes: F! Mo! US!).

Subspecies *vernonioides* is known only from Jalisco near Guadalajara. The one exact location would place it in the dissected canyon country to the NNE of the city.

REPRESENTATIVE SPECIMENS: México: Jalisco: Ixtlahuacán de los Membrillos, oak woodland, Detling 8775 (MICH); Rocky hills near Guadalajara, Pringle 2884 (F, GH, MEX, NY).

Eighteen morphological features on all nine available specimens of ssp. vernonioides and on 25 specimens of ssp. serratuloides were measured or scored. The two subspecies share many morphological features indicative of a close relationship. They differ in few characters as shown in Fig. 6. The treatment of these two taxa places emphasis on their similarities rather than on their differences.



of characters of Vernonia serratuloides flowers per head; B, length/width ra leaf blade. vernonioides (V). A, number of the involucre; D, length of the Ranges, means, and standard deviations and ssp. width of blade;

7. Vernonia autumnalis McVaugh, Contr. Univ. Mich. Herb. 9: 477. 1972. TYPE: México: Jalisco: 5 km S. of La Huerta, in oak forest, elev. 500-550 m, McVaugh 19833 (Holotype: MICH. Isotype: GA!).

Herbaceous perennial, 1-2 m; stems lanate sometimes becoming glabrate, striate. Leaves cauline; leaf blades 20-30 cm long, 6-15 cm wide (length/width ratio ca. 2.5), widest at or above the middle, elliptic-oblanceolate, glabrous above, lightly resinous to arachnoid below, apically acute, basally cuneate, margins revolute and remotely toothed, sometimes pinnately 4-lobed; petioles 1-2.7 cm long, glabrate to lanate. Inflorescences broadly pyramidal. Heads (4) 5-6 (7) flowered; peduncles ca. 5 mm long, lanate, sub-umbellate. Involucres campanulate (5) 6-9 mm high, (3.5) 4.5-5.2 mm wide; phyllaries arachnoid-ciliate, loosely appressed, purple; inner phyllaries elliptic-oblong, 6.5-8.2 mm long, 1.3-1.9 mm wide, tips acuminate; outer phyllaries lanceolate, 0.9-1.5 mm long, 0.7-0.9 mm wide. Pappus whitish; inner bristles 5.5-6.5 mm long, outer bristles 1-1.2 mm long. Corollas 8.8-10 mm long, reddishpurple, white glandular. Anthers 2.2-3.2 mm long. Achenes 2.7-3.6 mm long, pilose, 6-7 ribbed with 1 main rib on convex side. Chromosome number n = ca. 17. Flowering and fruiting occur from Oct. to Dec.

This species is found in southwestern Jalisco as shown in Fig. 3. It grows in ravines of oak-pine forest and tropical deciduous forest at 650 to 800 m elevation in the Northern Uplands of the Sierra Madre del Sur. *Mexia* 1575 from San Sebastián, Jalisco appears to be a hybrid between *V. autumnalis* and *V. bealliae*.

REPRESENTATIVE SPECIMENS: México: Jalisco: Mountainsides above (north of) La Cuesta, McVaugh 20268 (ENCB, MICH); 5 km N El Tuito, Mpio. de Cabo Corrientes, McVaugh 25476 (MICH).

8. Vernonia bealliae McVaugh, Contr. Univ. Mich. Herb. 9: 479. 1972. TYPE: México: Jalisco: San Sebastián, Nelson 4098 (Holotype: GH. Isotype: US!).

Vernonia corymbiformus sensu Gleas. Bull. New York Bot. Gard. 4: 198. 1906, not V. corymbiformis DC.

Suffruticose, erect or sometimes arching, 1.5-3 m; stems almost glabrous to lightly floccose. Leaves cauline; leaf blades (7) 9-14 (16) cm long, (2) 3-7 (10) cm wide (length/width ratio ca. 2-3), widest at or slightly below the middle, lanceolate to lanceolate-ovate, glabrous to somewhat scabrous above, reticulate-veined, resinous, with glandular trichomes to almost glabrous below, apically acuminate to almost acute, basally cuneate, margins serrate; petioles (0.7) 1-2 (3.5) cm long, glabrate to pilosehispid or almost tomentose. Inflorescences pyramidal, usually 1-3 dm wide. Heads 17-29 flowered; peduncles 1-3 cm long, strigose to resinous or glabrate, sub-umbellate in tight clusters. Involucres campanulate, (7.7) 9-11 (11.7) mm high, (5.5) 7-8 (8.3) mm wide; phyllaries glabrous, margins sometimes ciliate, loosely appressed, purple; inner phyllaries lanceolate, 6.3-9 mm long, 1-1.8 mm wide, tips awned, 0.2-1 mm long; outer phyllaries lanceolate, 2-5.6 mm long, 0.6-1.2 mm wide. Pappus white to straw colored; inner bristles 6-7 mm long, outer bristles 0.5-1.5 mm long. Corollas (8.5) 10-11.5 (12) mm long, reddish purple. Anthers (2.5) 3-4 mm long. Achenes ca. 4 mm long, densely white glandular when young, resinous when older. Flowering and fruiting occur from Feb. to May.

This species is distributed from Jalisco south to Michoacán as shown in Fig. 1. It grows in humid pine-oak-fir forests and barrancas on steep slopes and along streams, altitude 1620-2600 m, in the Northern Uplands of the Sierra de Parnaso, the Sierra de Perote, and Sierra de Coalcoman.

REPRESENTATIVE SPECIMENS: México: Jalisco: ca. 15 mi SE Autlán, McVaugh 10331 (duke, gh, mex, mich, ny, tex); Michoacán: S. Torricillas, Cealcoman, Hinton 13674 (f, mo, ny, us).

9. Vernonia barclayi H. Robinson & C. F. Reed. Phytologia 27: 52. 1973. TYPE: México: Sonora: Sierra Tecuari;

slopes above Rancho El Banco along road between Alamos and Mil Pilas, Chihuahua, A. S. Barclay & J. Arguellas 2018. (Holotype: US! Isotype: REED).

Plants frutescent, ca. 2 m tall; stems striate, whitish tomentose. Leaf blades 4-10 cm long, 1.5-3.5 cm wide (length/width ratio ca. 3) widest below the middle, oblongelliptic, downy above, tomentose below, apically acute, basally rounded, margins remotely and faintly toothed; petioles 2-3 mm long, whitish tomentose. Inflorescences subumbellate. Heads ca. 60 flowered; peduncles 1.5-2 cm long, whitish tomentose. Involucres campanulate, ca. 8 mm high, 10-12 mm wide; phyllaries arachnoid, tightly appressed in ca. 5 series, greenish with a slight tinge of purple; inner phyllaries lanceolate, ca. 6 mm long, ca. 1.5 mm wide, tips acuminate; outer phyllaries lanceolate, 2.5 mm long, 1 mm wide. Pappus whitish; inner bristles ca. 7 mm long, outer bristles 0.7 mm long. Corollas 12.5 mm long, reddish-purple. Anthers 3.5 mm long. Achenes 3.5 mm long, sparsely pilose-hispid, ca. 10 ribbed. Flowering and fruiting occur from April to May.

This species is known only from the type location in the state of Sonora along the road between Alamos, Sonora and Mil Pilas, Chihuahua (Fig. 5). It is locally abundant along moist ravines in the oak zone of Sierra Tecuari.

10. Vernonia feddemae McVaugh, Contr. Univ. Mich. Herb. 9(4): 480. 1972. TYPE: México: Tepic: ca. 5 km NE of Puga (ca. 15 km NE of Tepic), pastured lands among large boulders, with trees and shrubs, elev. ca. 1000 m, Feddema 846A (Holotype: MICH!).

Perennial herb, 1 m tall; stems striate, slightly pubescent. Leaves cauline, coriaceous; leaf blades 8-12 cm long, 3-5 cm wide (length/width ratio ca. 1.6-1.9), widest at the middle, elliptic, glabrate above, resinous-glandular and slightly downy below, apically acute, basally rounded-cuneate to slightly oblique, margins remotely toothed, revolute; petioles 2-5 mm long, downy. Inflorescences

pyramidal. Heads 3-5 flowered; peduncles ca. 1 cm long, pilose-hispid, multibracteate, almost subumbellate. Involucres cylindric, ca. 8 mm high, ca. 4 mm wide; phyllaries glandular-tomentose, loosely appressed, greenish-purple; inner phyllaries narrowly elliptic, ca. 4 mm long, ca. 1 mm wide, tips apiculate; outer phyllaries ovate, ca. 1.5 mm long, ca. 1 mm wide. Pappus whitish; inner bristles 4.5 mm long, outer bristles 0.9 mm long, scale-like. Corollas ca. 9 mm long, reddish-purple, white glandular. Anthers ca. 2.6 mm long. Achenes ca. 2.5 mm long, pilose, with ca. 9 or 10 ribs. Flowering and fruiting occur from August to September.

This species is known only from the type locality. This collection was made in pastured lands among large boulders, with trees and shrubs, at an elevation of ca. 1,000 m. As McVaugh (1972) noted, this species is related to others in the group by habit, but the repeated forking of the branches of the inflorescence and the long multibracteate peduncles are unique to this group and unique among Mexican Vernonias. All things considered, it is probably best placed among this group of Vernonias until other evidence suggests otherwise.

EXCLUDED SPECIES

Vernonia bolleana Sch. Bip. ex Seemann, Bot. Voy. Herald 297. 1856. TYPE: México: N. W. México, Seeman s.n. (Holotype: K! as photo MICH! Isotypes: P! G!). This species was placed by Gleason (1906) in subsection Paniculatae series Verae but it does not appear to belong here or in subsection Paniculatae series Umbelliformes. Most likely it should be placed in the genus Bolanosa.

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